Catalogue of American Amphibians and Reptiles.

Ernst, C.H., J.W. Gibbons, and M.E. Dorcas. 2002. *Regina*.

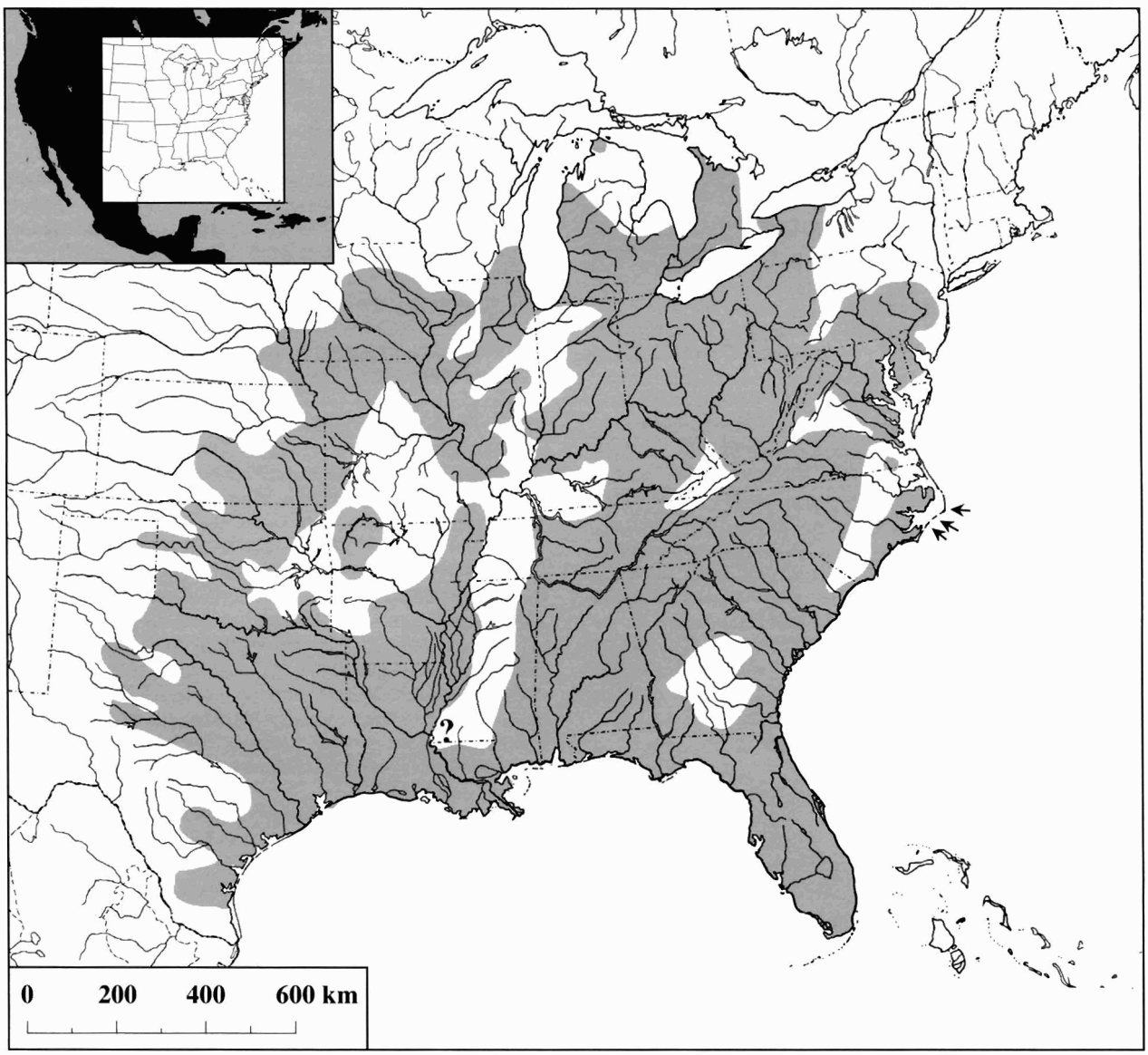
Regina Baird and Girard
Crayfish Snakes

Regina Baird and Girard 1853:45. Type species, *Coluber septemvittatus* Say 1825; designated by the International Commission on Zoological Nomenclature (1962:145).

Liodytes Cope 1885:194. Type species, *Helicops alleni* Garman 1874.

• **CONTENT.** Currently, four extant species, *Regina alleni*, *R. grahamii*, *R. rigida*, and *R. septemvittata*, and one fossil species, *R. intermedia*, are recognized, but a possible second fossil species, *Natrix hillmani*, may also belong to *Regina* (see **Fossil Record**). See also **Remarks**.

• **DEFINITION.** Snakes of the genus *Regina* are relatively short, semiaquatic, somewhat fossorial crayfish predators. Adult females are generally longer and stouter than adult males. Adult females have 118–178 ventrals, 47–87 subcaudals, and shorter tails that comprise 16–30% of body length. The shorter, more slender males have 110–175 ventrals, 55–89 subcaudals, and longer tails that comprise 17.5–34.0% of body length. The short head is slightly distinct from the neck, and comprises only 3.8–5.6% of body length. The nares are small and dorsolateral. Eye diameter is 14–17% of head length; the pupil is usually small, and makes up about 24–50% of eye diameter in adults (Rossman 1963). The nasal scale is partially divided by the naris, and the internasal scales are narrowed anteriorly (*R. alleni* has only one internasal scale). Present are a single loreal scale, 1–3 preoculars, 2–4 postoculars, 1 + 2(1–3) temporals, 6–9 supralabials, and 8–11 infralabials. The parietal scales may extend ventrolaterally between the postoculars and anterior temporal to narrowly touch the supralabials in some *R. alleni*. All *Regina*, except *R. alleni*, have keeled, pitless, dorsal body scales; those above the anal vent and on the tail of *R. alleni* may be slightly keeled (more prominent in males) with shallow pits. Body scale row counts



Map. Distribution of North American snakes of the genus *Regina*.

are: 19 (18–21) anterior, 19 (18–21) midbody, and 17 (15–19) preanal. The subcaudal scales lie in two rows. The cloacal scute (= anal plate) is divided. The single to slightly bilobed hemipenis extends 7–9 subcaudals, and bears 1–2 large basal hooks and a single sulcus spermaticus.

The dorsal body pattern usually consists of stripes of three colors (dark brown, black, or cream), with the paler lateral stripes located on the first and higher dorsal scale rows. The venter is either unmarked or has dark stripes, spots, or halfmoon-shaped marks. The head is unpatterned; the small labials lack dark bars, and no parietal spots are present.

The skull is moderately well developed, with the interorbital foramen situated below the frontals, but above the parasphenoid. The parasphenoid lacks a ventral keel, and the parietal bone lacks a posterior-medial ridge. The supratemporal is not reduced. The broad, flattened quadrate is little expanded dorsally. The basioccipital has no ventral process. Maxillary teeth are short, pointed to chisel-like, and may be gradually enlarged toward the rear of the series. No diastema is present. Tooth counts are: maxilla 20–29, dentary 24–35, palatine 11–18, and pterygoid 16–24. The vertebrae have well developed hypapophyses and relatively narrow transverse processes, which are anteroventral and rounded distally.

• **DESCRIPTIONS. General descriptions** of the four species are presented under the generic names *Liodytes* or *Natrix* in Wright and Wright (1957), and in Ernst and Barbour (1989), Conant and Collins (1998), Tennant and Bartlett (2000), Ernst and Ernst (2003), and Gibbons and Dorcas (2003) under *Regina*. **Dorsal scale microdermatoglyphics** were described by Price (1982, 1983).

• **ILLUSTRATIONS. Color or black and white illustrations** of the four species are included in Wright and Wright (1957), Ernst and Barbour (1989), Conant and Collins (1998), Tennant and Bartlett (2000), Ernst and Ernst (2003), and Gibbons and Dorcas (2003). The **hemipenis** of three species is illustrated in Cope (1900), and Rossman (1963) illustrated the **teeth**.

• **DISTRIBUTION.** The genus is entirely North American, and is represented by four species that range from western New York and western Pennsylvania, southwestern Ontario, southern Michigan, Illinois, southeastern Wisconsin, Iowa, and southeastern Nebraska south through peninsular Florida, and to the Gulf Coast of Florida, Alabama, and Mississippi in the east, and through northern and western Missouri, eastern Kansas, Oklahoma, southern and eastern Arkansas, and Louisiana to the Gulf Coast of eastern Texas in the west. These snakes are absent from most of the Ozark Plateau and Ouachita Mountains of Missouri, Arkansas, and eastern Oklahoma; the eastern floodplain of the Mississippi River from southern Illinois to Mississippi; western Indiana, central Illinois, and western Kentucky; the Appalachian Mountains of western Virginia, southwestern West Virginia, and adjacent Kentucky; southeastern Virginia and the piedmont of North Carolina; and southcentral Georgia (see species accounts for individual maps).

• **FOSSIL RECORD.** Fossils referable to individuals of the genus *Regina* have been found at a Pliocene (Blancan) site in Nebraska, Pleistocene (Irvingtonian) sites in Florida and Nebraska, and Pleistocene (Rancholabrean) deposits in Georgia, Kansas, Pennsylvania, and Virginia (Holman 1995, 2000); see species accounts for details.

Meylan (1982) named the early Pleistocene (Irvingtonian) species *R. intermedia* (holotype, University of Florida 26383, examined by CHE) from dentary and vertebral remains found at the Inglis IA Site, Citrus County, Florida. The dental characters are intermediate between those of *R. alleni* and *R. rigida* and those of *R. grahamii* and *R. septemvittata*. Meylan (1982) also indicated that *Nerodia hillmani* Wilson 1968 from the Lower Pliocene Ogallala Formation of Trego County, Kansas may be referable to *Regina*.

• **PERTINENT LITERATURE. General accounts** of the four species are in Wright and Wright (1957), Ernst and Barbour (1989) and Ernst and Ernst (2003). Important **life history studies** include those of Hall (1969), Branson and Baker (1974), Franz (1977), Godley (1980, 1982), Godley et al. (1984), and Seigel (1992). Other topics include: **systematics, taxonomy, and evolution** (Bogert 1940; Smith and Huheey 1960; Dessauer et al. 1962; Rossman 1963, 1985; Price 1983; Marx and Rabb 1972; Rossman et al. 1982; Alfaro and Arnold 2001, see also **Remarks**), **karyotype** (Eberle 1972, Kilpatrick and Zimmerman 1973), **blood chemistry** (Dessauer 1970), **morphology** (Marx and Rabb 1972), **skull** (Dwyer and Kaiser 1997), **lungs** (Wallach 1998), **tooth structure** (Rojas and Godley 1979), **scales** (Cliburn 1958; Price 1982, 1983), **life history strategy** (Dunham et al. 1988), **stereotyped behavior** (Carpenter and Ferguson 1977), **diet and feeding behavior** (Franz 1976, Godley et al. 1984, Myer 1987), and **vernacular name** (Frank and Ramus 1995).

Because of the wide distribution of these snakes, members of the genus are included in many general works or in numerous state or regional guides and checklists (see species accounts).

• **KEY TO THE SPECIES.** The parenthetical number refers to the species account for that taxon.

1. a. Dorsal body scales smooth, one internasal scale present, no dark pigment on venter ..... *R. alleni*
   b. Dorsal body scales keeled, two internasal scales present, venter with dark stripes or no dark pigment 2

2. a. A single dark median stripe on venter, or no dark pigment present ..... *R. grahamii*
   b. Two dark longitudinal stripes or rows of halfmoons on the venter 3

3. a. Venter with two longitudinal rows of halfmoons, lower dorsal scale rows smooth ..... *R. rigida*
   b. Venter with two longitudinal stripes not divided into halfmoons, lower dorsal scale rows keeled .... *R. septemvittata* (757)

• **REMARKS.** Alfaro and Arnold (2001) examined the mitochondrial DNA of the species currently assigned to *Regina* and of other thamnophiine snakes. The genus *Regina* was found to be polyphyletic. *R. grahamii* and *R. septemvittata* are allied with watersnakes in the genus *Nerodia*, with *R. grahamii* closely related to *Tropidoclonion lineatum*. In contrast, *R. alleni* and *R. rigida* belong to the semifossorial clade of thamnophiinaes, which includes the genera *Clonophis, Seminatrix, Storeria* and *Virginia*. *Seminatrix pygaea* seems to be the closest relative to *R. alleni* and *R. rigida*.

Alfaro and Arnold's (2001) groupings within *Regina* match those noted previously with regard to feeding adaptations and behavior by Rossman (1963), Franz (1976, 1977), Rojas and Godley (1979), Myer (1987), and Dwyer and Kaiser (1997). Alfaro and Arnold (2001) did not propose immediate taxonomic changes, but suggested that a reevaluation of the taxonomic status of the genus *Regina* is warranted.

• **NOMENCLATURAL HISTORY.** The first species now assigned to the genus *Regina*, *R. septemvittata* and *R. rigida*, were described and placed in the then broad-based genus *Coluber*

by Say (1825). Holbrook (1842) considered *Coluber leberis* Linnaeus 1758 a senior synonym of *Coluber septemvittata* Say 1825, and included it and *Coluber rigidus* Say 1825 in the genus *Tropidonotis* Kuhl 1824. Baird and Girard (1853) created the genus *Regina*, including in it *R. leberis*, *R. rigida*, and the new *R. grahamii*. In 1874, Garman included these three species in the genus *Helicops* Wagler 1830, and described the species *H. alleni*, but Cope (1888) thought *H. alleni* sufficiently different from other *Helicops* to be placed in the genus *Liodytes* Cope 1885. In 1892, Cope assigned *grahamii, rigida,* and *septemvittata* to the comprehensive genus *Natrix*, which included all New and Old World water snakes. The species *alleni* remained in the genus *Liodytes* until 1963 when Rossman presented morphological evidence to show that it and *N. grahamii, N. rigida*, and *N. septemvittata* were sufficiently different to be separated from the New World *Natrix* [= *Nerodia*] and placed in his resurrected genus *Regina*.

Price (1983) suggested that, on the basis of different dorsal scale microdermatoglyphics, *Regina* should be divided into two genera, *Liodytes* and *Regina*. He redefined *rigida* and placed it with *alleni* in *Liodytes* on the basis of their similar dorsal scale microsculpturing and fewer subcaudal and ventral scales, but left *grahamii* and *septemvittata* in *Regina*, because they have higher subcaudal and ventral counts and the patterns of their dorsal scale surfaces more closely resemble those of watersnakes in the genus *Nerodia*. His further definition of *Liodytes* included most of the characters listed by Rossman (1963) for *Regina*. Rossman (1985) discussed the great overlap in significant characters between Price's *Liodytes* and Rossman's *Regina*, pointing out that the only exclusionary characters introduced by Price were the scale microdermatoglyphic patterns, low subcaudal and ventral numbers, and a more restricted definition of tooth shape. *Regina septemvittata* has ventral numbers that overlap those of both *alleni* and *rigida*, and *grahamii* has similar subcaudal counts to those of *alleni* and *rigida*. So, these characters are useless for dividing the genus *Regina*. Also, the differences in tooth morphology (see Rossman 1963 and Rojas and Godley 1979 for details) are probably clinal and represent a greater dependence on a crayfish diet, with the shorter, stouter teeth of *grahamii* and *septemvittata* representing early development, and those of *alleni* and *rigida* later morphology in the same cline. Much convergence occurs in snake dorsal scale microdermatoglyphics and these are poor taxonomic characters (Blaney 1977). In addition, the lower surface ornamentation on the dorsal scales of *alleni* and *rigida* are possibly adaptations associated with more highly developed burrowing behavior than is known in *grahamii* and *septemvittata* (Blaney 1977). On the basis of many important shared characters and few defining characters, Rossman (1985) proposed to retain *alleni* and *rigida* in the genus *Regina*.

• **ETYMOLOGY.** The generic name *Regina* is a Latin feminine name meaning royal or queen.

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Primary editor for this account, Larry David Wilson.

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